South African Journal of Botany 103 (2016) 193–209

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Seedling recruitment responses to interventions in seed-based ecological restoration of Peninsula Shale Renosterveld, Cape Town

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ARTICLE INFO

Article history:
Received 5 May 2015
Received in revised form 2 September 2015
Accepted 3 September 2015
Available online 5 December 2015

Edited by RM Cowling

Keywords:
Critically Endangered ecosystem
Old fields
Alien plant species
Invasive annual grasses
Seedling emergence
Seedling survival

ABSTRACT

Peninsula Shale Renosterveld, a Critically Endangered ecosystem, requires ecological restoration intervention on transformed areas. Yet there is little guidance due to very few renosterveld studies and limited knowledge of the mechanisms driving ecological responses. This study set out to test the effects of 32 interventions, comprised of five crossed factors (seeding of 31 species, fire, tillage, herbicide application and rodent exclusion), on vegetation recruitment on a site dominated by alien, annual grasses. Actual experimental responses were compared with predicted responses presented in an *a priori* ecological-response model. Responses to the interventions were highly variable. Sowing on its own was almost ineffectual, but restoration of species was enhanced when seeding was implemented with one or more of the other factors. In combination with other treatments, seeding made significant contributions to overall seedling density, species richness and canopy cover and is imperative if this ecosystem is to recover from extensive alien grass invasion. Several three- to five-factor interventions resulted in a full set of desired responses. Half of the responses predicted in an ecological-response model were confirmed. Study outcomes have the potential to guide future research and implementation of larger scale renosterveld restoration.

1. Introduction

In ecological restoration the implementation of interventions may be necessary to overcome ecosystem degradation and initiate ecosystem recovery (Hobbs and Cramer, 2008; Brudvig, 2011). In Peninsula Shale Renosterveld, a Critically Endangered ecosystem with a conservation target shortfall (DEA, 2011), succession following alien plant clearing is characterised by poor colonisation of indigenous species (Terblanche, 2011). In transformed areas, the seed bank is in general depleted and dominated by alien species (Cowan, 2013) making the implementation of restoration interventions necessary to facilitate recovery.

Renosterveld has been dramatically impacted by the extinctions of large herbivores within 200 km of Cape Town by the early 1700s (Skead, 1980), extensive agricultural transformation by European settlers by the late 1800s, alteration of natural fire regimes (Rebelo, 1995; Krug et al., 2004) and alien plant invasions (Milton, 2004; Helme and Rebelo, 2005; Musil et al., 2005). There is consequently a high level of uncertainty about how to restore renosterveld due to an absence of baseline data and reference sites to provide restoration benchmarks (Rebelo, 1995; Milton, 2007).

There are few studies on renosterveld restoration despite increased attention in recent years. Studies have addressed the roles of, *inter alia*, fire (Midoko-Iponga, 2004; Musil et al., 2005; Memiaghe, 2008; Radloff, 2008; Curtis, 2013; Heelemann et al., 2013), grazing (Midoko-Iponga, 2004; Midoko-Iponga et al., 2005; Radloff, 2008; Curtis, 2013), competition (Midoko-Iponga, 2004; Musil et al., 2005; Memiaghe, 2008; Muhl, 2008; Sharma et al., 2010; Terblanche, 2011), and plant reintroduction using seed (Holmes, 2002; Midoko-Iponga, 2004), rooted material (Holmes, 2002) and seedlings (Midoko-Iponga, 2004). Interactions between some of the above-mentioned factors have been investigated, for instance fire, seeding/propagated seedlings and grazing/grass-clearing/herbicide (Midoko-Iponga, 2004; Midoko-Iponga et al., 2005; Musil et al., 2005; Memiaghe, 2008; Curtis, 2013) yet more than three factors have not been tested in a factorial manner to determine the effects of multiple resultant interactions on ecosystem regeneration. The few renosterveld restoration studies testing the reintroduction of seed have achieved limited success (Holmes, 2002, 2005; Midoko-Iponga, 2004). Seed and seedling consumption by small mammals has been identified as influencing renosterveld restoration (Holmes, 2002; Dreyer, 2012) but has not been empirically tested.

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http://dx.doi.org/10.1016/j.sajb.2015.09.009

Table 1
Ecological-response model of predicted responses to restoration interventions where '+' = increase, '0' = no change and '−' = decrease.

Intervention	Seeded species		Existing Indigenous species		Weed species	
Burning	Density	+	Density	+		
	Richness	+	Richness	+		
	Cover	+	Cover	+	Cover	+
	Height	+				
Tillage	Density	+	Density	−		
	Richness	+	Richness	−		
	Cover	+	Cover	−	Cover	+
	Height	+				
Herbicide application	Density	+	Density	−		
	Richness	+	Richness	−		
	Cover	+	Cover	−	Cover	−
	Height	+				
Rodent exclusion	Density	+	Density	0		
	Richness	+	Richness	0		
	Cover	+	Cover	0	Cover	0
	Height	+				
Seeding	Density	+	Density	0		
	Richness	+	Richness	0		
	Cover	+	Cover	0	Cover	0
	Height	+				

Holmes and Richardson (1999) emphasise the importance of ecological principles of regeneration in developing restoration protocols to optimise restoration outcomes for fynbos and other fire-driven temperate shrublands. Based on current understanding, restoration interventions, designed to mimic ecosystem drivers, are recommended for implementation in restoration: fire, to stimulate germination of the soil-stored seed bank and emergence of resprouting species (Holmes and Richardson, 1999); and soil disturbance to create safe sites for seed to germinate (Milton, 2007). Other interventions which may drive ecological responses include seeding, to supplement guilds which are under-represented or absent (Holmes and Richardson, 1999; Holmes, 2002; Helme and Rebelo, 2005); herbicide application, to reduce competition from invasive alien species (Holmes and Richardson, 1999; Musil et al., 2005; Milton, 2007); and management of small mammals, to reduce granivory and herbivory (Holmes, 2002).

However our understanding of the mechanisms underpinning these drivers is deficient (Rebelo et al., 2006) as reflected by the limited success in renosterveld restoration efforts to date. Based on the literature and local expert opinion and adapted from increaser–decreaser models (e.g. Milton, 2007), we test an *a priori* ecological-response model which has been simplified to predict the majority response of the community within the first season following the implementation of interventions (burning, tillage, herbicide application, rodent exclusion and seeding) as surrogates to ecological drivers (Table 1).

In addition this study tested the response of seedling recruitment to multifactorial treatment combinations (henceforth interventions) with five main treatments (burning, tillage, herbicide application, seeding and rodent exclusion).

2. Methods

2.1. Study area

Peninsula Shale Renosterveld occurs within the lowlands of the Cape Floristic Region (von Hase et al., 2003; Rebelo et al., 2006) at the south western tip of Africa (Manning and Goldblatt, 2012). The Cape Floristic Region is one of 34 internationally recognised biodiversity hotspots due to extensive habitat loss (Mittermeier et al., 2005) coupled with exceptionally high levels of floristic diversity and endemism (Manning and Goldblatt, 2012). Renosterveld types largely experience a Mediterranean-type climate (Taylor, 1980) and are associated with relatively fertile, clay-rich soils (von Hase et al., 2003). Peninsula Shale Renosterveld is described as a tall, open shrubland and grassland occurring on gentle to steep gradients and remnants of the vegetation type are situated either side of the Cape Town city bowl on the Cape Peninsula (Rebelo et al., 2006).

2.2. Field trial

The field experiment was situated in the game camp in Groote Schuur Estate (33°56′53.57″S, 18°27′56.34″E, 43 m amsl) within Table Mountain National Park on the north-eastern slopes of Devil's Peak (Fig. 1). The burnt and unburnt plots were consolidated into two blocks located on gradual slopes (gradient greater than 1:10). Grazing by introduced resident large herbivores was removed from the experimental plots following recommendations of Helme and Rebelo (2005) to remove domestic livestock from renosterveld post-fire to prevent herbivory and trampling.

2.3. Experimental design

The experimental design is complete factorial. Five factors (burning, tillage, herbicide application, rodent exclusion and seeding) at two levels (implemented and not implemented) were crossed resulting in 32 interventions, including the control, and replicated four times. Burnt and unburnt plots were consolidated into two blocks. Seeded plots were arranged in alternate rows yet sown as individual units. Tillage, herbicide application and rodent-exclosure treatments were arranged randomly. From this point, the interventions are referred to with acronyms (Table 2).

2.4. Target species selection and collection

In order to select species for plant functional diversity, ecosystem functioning and resilience (Holmes and Richardson, 1999; Diaz and Cadibo, 2001; Funk et al., 2008; Clewell and Aronson, 2013), a comprehensive list of species occurring within Peninsula Shale Renosterveld was compiled and arranged according to growth forms. For the purpose of this study, however, remnants on Signal Hill and Devil's Peak were assessed to reduce the species list from 668 species to a more manageable number according to population location, population size and the likelihood of populations producing adequate seed within the time-frame identified. Although collection of as many species as possible is recommended for restoration of fynbos and other fire-adapted shrublands (Holmes and Richardson, 1999), it was decided that approximately 25–35 species would be appropriate for this study. Seed was ultimately collected from 31 species, representing 14 families and six growth forms (Table 3).

2.5. Initial seed processing and storage

Seeds from most species were collected from remnant areas from October 2011 to February 2012 with several species being collected in May 2012. The seed was temporarily kept in a well-ventilated room and fumigated with insecticide (Doom Fogger) prior to storage at 15% RH and 15°C for approximately 4 months. The seed for all species was partially cleaned (debris removed yet covering structures retained) with the exception of *Myrsine africana* which was soaked and the flesh removed by rubbing in a sieve.

2.6. Intervention implementation

The Newlands Working on Fire team prepared a 20 m perimeter firebreak and implemented the prescribed burn on 26th March

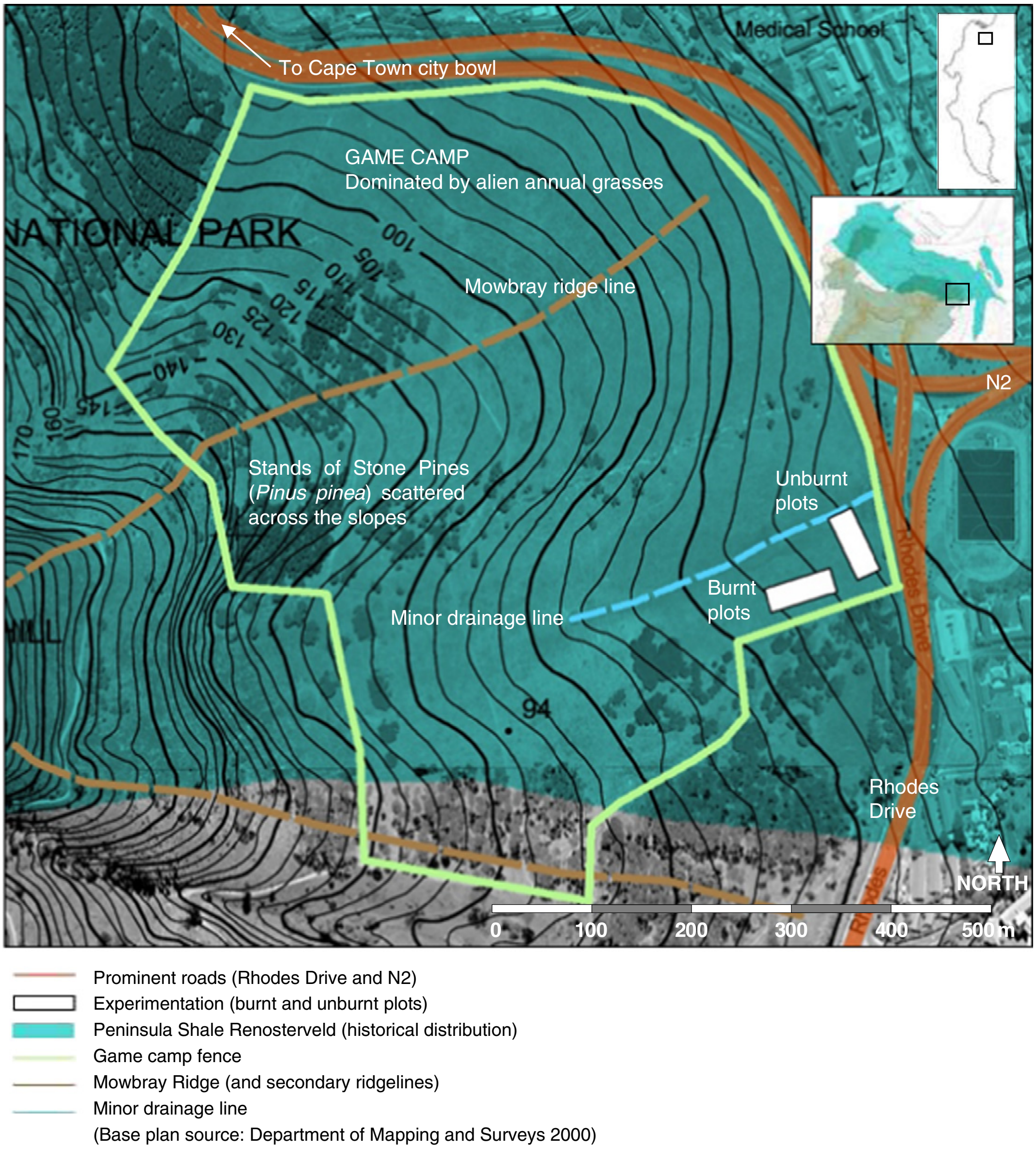

Fig. 1. Field-experiment study area. Position of the experimental field site (burnt and unburnt blocks) within the game camp of Groote Schuur Estate incorporated into Table Mountain National Park.

Table 2
Intervention acronyms. Five factors at two levels were crossed to produce 32 interventions: C = control, S = seeding, B = burning, T = tillage, H = herbicide application and R = rodent exclusion.

Unseeded interventions		Seeded interventions	
1.	C	17.	S
2.	B	18.	BS
3.	T	19.	TS
4.	H	20.	HS
5.	R	21.	RS
6.	BT	22.	BTS
7.	BH	23.	BHS
8.	TH	24.	THS
9.	BR	25.	BRS
10.	TR	26.	TRS
11.	HR	27.	HRS
12.	BTH	28.	BTHS
13.	BTR	29.	BTRS
14.	BHR	30.	BHRS
15.	THR	31.	THRS
16.	BTHR	32.	BTHRS

2012. The fire was ignited and promoted by a diesel–petrol mix, applied sparingly across the area (81 × 21 m). The low biomass, consisting predominantly of alien, annual grass litter, burnt rapidly. The area burned evenly and burnt out within 11 min. Once burnt, the plots were measured, pegged, demarcated and labelled. Each intervention was implemented in a 25 m^2 plot (5 × 5 m) with a 9 m^2 core plot (3 × 3 m). Each block (burnt and unburnt) was fenced to prevent herbivory from the five resident Zebra (*Equus sp.*). Trenching along the fence lines enabled the extension of the fencing mesh to 300 mm below ground level to exclude porcupine (*Hystrix africaeaustralis*) which target roots, bulbs and tubers (Stuart and Stuart, 2007). The fencing mesh apertures were large enough to permit small mammals passage (50 × 50 mm diamond mesh). Tillage commenced with the first rains in the second week of April 2012 and was completed by the end of the month. Tillage was carried out by hand and entailed turning the soil to the depth of a garden fork (approximately 150 mm). Herbicide (non-specific, post-emergent glyphosate, 'Round-up 360' by Dow Agro-Sciences) was applied on 7th and 8th May 2012 in low wind conditions and a

Table 3
Seed was collected from 31 species representing six growth forms (five graminoids, five geophytes, three forbs, four succulent shrubs, 10 low shrubs and four tall shrubs).

Species	Family	Growth form
Arctopus echinatus	Apiaceae	Forb
Athanasia crithmifolia	Asteraceae	Tall shrub
Babiana fragrans	Iridaceae	Geophyte
Chironia baccifera	Gentianaceae	Low shrub
Chrysocoma coma-aurea	Asteraceae	Low shrub
Cymbopogon marginatus	Poaceae	Graminoid
Dimorphotheca pluvialis	Asteraceae	Forb (annual)
Ehrharta calycina	Poaceae	Graminoid
Erepsia anceps	Mesembryanthemaceae	Succulent shrub
Eriocephalus africanus var. *africanus*	Asteraceae	Low shrub
Felicia filifolia	Asteraceae	Low shrub
Helichrysum cymosum subsp. *cymosum*	Asteraceae	Low shrub
Helichrysum patulum	Asteraceae	Low shrub
Hermannia hyssopifolia	Malvaceae	Low shrub
Lachenalia fistulosa	Hyacinthaceae	Geophyte
Lampranthus emarginatus	Mesembryanthemaceae	Succulent shrub
Moraea bellendenii	Iridaceae	Geophyte
Myrsine africana	Myrsinaceae	Tall shrub
Ornithogalum thyrsoides	Hyacinthaceae	Geophyte
Othonna arborescens	Asteraceae	Succulent shrub
Pelargonium cucullatum subsp. *tabulare*	Geraniaceae	Low shrub
Pentameris airoides subsp. *airoides*	Poaceae	Graminoid (annual)
Podalyria sericea	Fabaceae	Low shrub
Ruschia rubricaulis	Mesembryanthemaceae	Succulent shrub
Salvia africana-caerulea	Lamiaceae	Low shrub
Searsia laevigata var. *villosa*	Anacardiaceae	Tall shrub
Searsia tomentosa	Anacardiaceae	Tall shrub
Tenaxia stricta	Poaceae	Graminoid
Themeda triandra	Poaceae	Graminoid
Trachyandra muricata	Asphodelaceae	Geophyte
Ursinia anthemoides subsp. *anthemoides*	Asteraceae	Forb (annual)

rectangular hood was attached to the lance to minimise drift into neighbouring plots (See Photo Plate 1.).

Allowing for a breakdown period of 11 days the seed mix was broadcast sown into each of the 64 plots on 19th and 20th May 2012. During the two weeks prior to sowing, the seed was weighed, divided into 64 portions and placed into 5 ℓ containers whilst the three species requiring hot water treatment (*Arctopus echinatus*, *M. africana* and *Podalyria sericea*) were similarly weighed, divided and placed into 64 small, cotton bags in preparation for soaking. A final collection of potentially recalcitrant seed was collected on 15th May 2012, weighed, divided and placed into the 64 containers. To promote germination (Brown and Botha, 2004), on 16th and 17th May 2012 the 64 containers and cotton bags were placed in batches in the Kirstenbosch smoke tent filled with smoke derived from wet and dry fynbos material and the smoke allowed to settle for 3 h. The night prior to sowing, the cotton bags were placed in 80 °C water and allowed to cool and soak overnight (10 h).

On sowing, on a plot-by-plot basis, each 5 l container of seed mix received seed from one cotton bag, was topped-up with approximately 2.5 l of horticultural sand, moistened with a water-fungicide dilution ('Apron XL' with active ingredient mefenoxam, 1 ml/3 kg seed) and thoroughly stirred. The moist sand–seed mix from one container was hand broadcast into one 25 m^2 plot at a rate of approximately 57.42 kg semi-cleaned seed per hectare and the area lightly swept with a stiff broom to promote soil-seed contact.

Immediately thereafter, the rodent-exclusion cages were placed over the 1 m^2 subplots and secured in place with wire pegs (See Photo Plate 2.). Each cage protected an area just larger than the 1 m^2 subplot (approximately 1.2 × 1.2 m), measured approximately 0.5 m high and had a horizontal perimeter skirt at the base of the cage of approximately 0.25 m to discourage rodents from burrowing underneath. Each cage was cut with an angle grinder from two sheets of ungalvanised, mild steel mesh, bent into shape and the seams pop-riveted. Mesh with a very small aperture size of 3 × 6 mm was selected in order to exclude even the smallest granivorous rodents expected to occur on the site, the Pygmy Mouse (*Mus minutoides*). The interventions were fully implemented by 20th May 2012.

With the aim of reducing the seed set from the dominant invasive annual grasses, *Avena fatua*, *Briza maxima* and *Briza minor*, in October 2012 the grasses in all plots were brushcut to a height of approximately 400 mm as the presence of indigenous seedlings prevented cutting closer to the ground. The effect of this was not measured but it appeared to be ineffectual particularly with respect to the *A. fatua* plants which subsequently produced inflorescences.

2.7. Data collection

Data were collected from 128 plots (32 interventions replicated four times). One 1 m^2 subplot was sampled from each of the rodent-exclusion plots, as only one cage was installed per plot, whilst two 1 m^2 subplots were sampled from the plots without rodent exclusion resulting in a total of 192 (1 m^2) subplot samples per data collection. The subplots were initially randomly selected and thereafter repeatedly sampled. Four data collections took place and occurred in alternate months starting July 2012 (two months since sowing) and ending January 2013 (eight months since sowing). Data were collected for the following per 1 m^2 quadrat: number of plants per species (comprised of seedlings and resprouts) and percentage canopy cover per species for the existing indigenous species; number of seedlings per species, height of five seedlings per species and percentage canopy cover per species for the 31 seeded species; and, a combined canopy cover measurement was taken for the weed species. Height and canopy cover were not recorded in the first data collection. All existing indigenous species and seeded species and were counted individually except the seeded *Chrysocoma coma-aurea* and *Felicia filifolia* seedlings which were combined due to their seedlings being indistinguishable.

2.8. Data analysis

Data were analysed with respect to eight response variables: seeded species (seedling density, species richness, canopy cover and seedling height), existing indigenous species (plant density, species richness and canopy cover) and weed species (canopy cover) (Tables 4 and 5). Where data was analysed from multiple collections, the data were pooled due to the short time span of the experiment which focussed specifically on seedling emergence.

2.8.1. Seeded species

Seedling density and species richness data from all four data collections were analysed whilst canopy cover and seedling height data were analysed from the September 2012, November 2012 and January 2013 data collections. The data from the two 1 m^2 subplots per intervention were averaged (except in rodent-exclosure plots where there was only one 1 m^2 subplot). Each of the four data sets were positively skewed due to the experimental design where half of the plots were unseeded resulting in a high proportion of zero values. As such, no data sets could be adequately transformed. Consequently, to establish the effect of seeding versus not seeding on each of the response variables, a Kruskal–Wallis test was run with the group factor S (seeding). Three additional Kruskal–Wallis tests were run to ascertain the effect of seeding on the overall indigenous community with respect to density, richness and canopy cover (for two response variables: existing indigenous species, and, existing indigenous species plus seeded species). Thereafter, data from the unseeded plots were deleted from the respective data sets, reducing the analysis from 32 interventions to the 16 seeded interventions. The seeded-only data were acceptably transformed for each response variable. Once transformed, a general ANOVA was run to

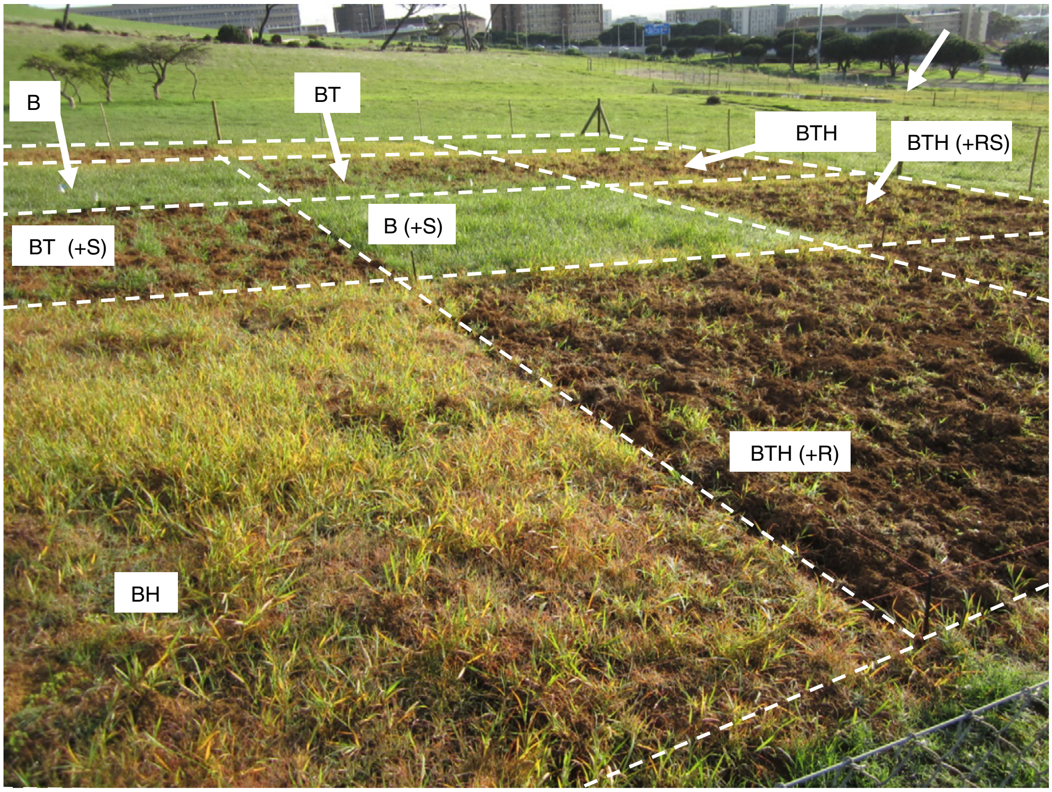

Photo Plate 1. The matrix of interventions partially implemented in the burnt block. Tillage initially reduced grass cover exposing the soil and providing safe sites for seed germination. Once tilled, herbicide was applied, seen here the yellowing effect is starting to show (left foreground). Seeding and rodent-exclusion interventions yet to be implemented are indicated in brackets. The unburnt block is just visible top right (arrow) (photo taken early May 2012).

determine the main effects and all interaction effects for burn, tillage, herbicide application and rodent exclusion and Tukey post-hoc tests were run. In the analysis of seedling height, *in lieu* of averaging the median height (cm) across all of the species recorded in a subplot, it was deemed more accurate to use the height of the Chryso-Fel category (*C. coma-aurea* and *F. filifolia* seedlings) as a surrogate for seedling height as these seedlings were recorded in most plots over the four data collections.

Photo Plate 2. Once seeded, rodent-exclusion cages were placed over each 1 m^2 subplot and pegged in place.

Table 4
Summary table for the 16 seeded and 16 unseeded interventions including variance ratio (F) and statistical probability derived from general ANOVA. For density, richness, cover and height of seeded species of the seeding-only intervention, chi squared (χ^2) and statistical probability are derived from Kruskal–Wallis tests.

	Seeded interventions							
	Seeded species				Existing indigenous species			Weed species
	Density	Richness	Cover	Height	Density	Richness	Cover	Cover
	Fourth root transformed	Square root transformed	Fourth root transformed	Square root transformed	Square root transformed	Untransformed	Third root transformed	Arcsine transformed
S	$\chi^2 = 298.30^{***}$	$\chi^2 = 298.30^{***}$	$\chi^2 = 204.10^{***}$	$\chi^2 = 250.90^{***}$	F = 0.53	$F = 4.77^{*}$	F = 1.16	F = 0.78
BS	$F = 5.52^{*}$	$F = 14.17^{***}$	F = 0.00	F = 3.23	F = 2.30	F = 0.04	F = 0.01	F = 0.00
TS	$F = 201.64^{***}$	$F = 166.60^{***}$	$F = 87.28^{***}$	F = 0.39	F = 0.04	F = 0.04	F = 0.00	F = 0.39
HS	$F = 103.26^{***}$	$F = 109.22^{***}$	$F = 162.19^{***}$	$F = 65.43^{***}$	F = 2.33	F = 0.59	F = 0.01	F = 1.97
RS	$F = 7.27^{**}$	F = 0.03	$F = 5.63^{*}$	F = 1.68	F = 0.05	F = 2.00	F = 0.07	F = 0.54
BTS	F = 2.74	$F = 4.76^{*}$	F = 0.27	F = 0.09	F = 0.66	F = 1.06	F = 0.40	F = 0.94
BHS	F = 0.65	F = 0.09	F = 2.04	F = 1.04	F = 0.19	F = 0.70	F = 0.64	F = 0.29
THS	$F = 21.13^{***}$	$F = 43.91^{***}$	$F = 32.50^{***}$	$F = 9.56^{**}$	F = 0.31	F = 0.70	F = 0.13	F = 0.53
BRS	F = 0.00	F = 1.08	F = 0.31	$F = 6.81^{*}$	F = 2.46	F = 1.19	F = 1.89	F = 0.01
TRS	F = 1.27	F = 2.67	$F = 4.09^{*}$	F = 0.00	F = 0.20	F = 2.58	F = 0.25	F = 0.20
HRS	$F = 3.91^{*}$	$F = 8.17^{**}$	F = 0.94	F = 2.17	F = 0.00	F = 1.06	F = 0.08	F = 1.02
BTHS	F = 0.00	F = 0.45	F = 0.00	F = 0.12	F = 0.14	F = 1.65	F = 0.01	F = 1.51
BTRS	$F = 5.11^{*}$	F = 0.27	F = 3.60	$F = 4.65^{*}$	F = 0.10	F = 2.38	F = 0.71	F = 0.04
BHRS	F = 0.90	F = 0.00	F = 0.07	F = 0.60	F = 0.04	F = 0.50	F = 0.15	F = 1.37
THRS	F = 0.03	F = 0.08	F = 0.38	F = 3.52	F = 0.21	F = 1.49	F = 0.88	F = 0.06
BTHRS	$F = 8.18^{**}$	$F = 7.38^{**}$	F = 1.42	Unbalanced	F = 2.20	F = 0.26	F = 0.99	F = 0.11
	Unseeded interventions							
	Seeded species				Existing indigenous species			Weed species
	Density 4th root transformed	Richness square root transformed	Cover fourth root transformed	Height square root transformed	Density square root transformed	Richness untransformed	Cover third root transformed	Cover arcsine transformed
C								
B					$F = 161.16^{***}$	$F = 66.56^{***}$	$F = 4.25^{*}$	$F = 18.44^{***}$
T					$F = 65.13^{***}$	$F = 47.24^{***}$	$F = 5.86^{*}$	F = 0.24
H					F = 0.01	$F = 5.35^{*}$	$F = 16.79^{***}$	$F = 200.30^{***}$
R					$F = 8.79^{**}$	F = 0.00	F = 2.44	$F = 48.28^{***}$
BT					F = 0.23	F = 3.24	F = 1.49	$F = 8.76^{**}$
BH					$F = 6.13^{*}$	F = 0.33	F = 0.01	$F = 7.24^{**}$
TH					F = 1.49	F = 0.10	F = 0.26	$F = 33.30^{***}$
BR					F = 0.01	F = 3.47	F = 0.67	F = 0.64
TR					F = 3.36	F = 0.33	F = 1.07	$F = 6.53^{*}$
HR					$F = 20.27^{***}$	F = 2.38	F = 2.35	F = 2.04
BTH					F = 0.92	$F = 7.28^{**}$	F = 2.34	F = 0.39
BTR					F = 0.07	F = 0.07	F = 0.07	F = 1.99
BHR					F = 0.51	F = 0.93	F = 0.00	F = 2.57
THR					F = 0.05	F = 0.70	F = 0.05	F = 3.70
BTHR					F = 3.23	F = 0.15	F = 0.05	F = 0.02

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

In addition, seedling survival of the 31 seeded species from the September 2012, November 2012 and January 2013 data collections were analysed with respect to survival per growth form and per intervention.

2.8.2. Existing indigenous species

Existing indigenous species were analysed with respect to plant density (from September 2012), species richness (from September 2012) and canopy cover (from September 2012, November 2012 and January 2013), using data from all plots (seeded and unseeded). General ANOVA analyses were run for the main factors (burning, tillage, herbicide application, rodent exclusion and seeding) and all interactions.

2.8.3. Weed species

Data were analysed from all plots (seeded and unseeded) from the November 2012 time point only due to an inability to successfully transform the data from the three data collections (September 2012, November 2012 and January 2013). The November data were selected as weed cover was greatest during this time point. A general ANOVA was run on arcsine transformed data for the main factors and all interactions.

2.9. Limitations

Several locational, spatial and cost constraints informed the in-field layout of the experimentation whereby the burnt and unburnt plots were consolidated into two blocks out of necessity. Given the consolidation, the statistical analyses did not account for unwanted influence of extraneous environmental variables resulting from field effects. The measured effects of the burn may not be due to the burn alone but may in part be due to other environmental variables which were not tested.

The span of the study, encompassing eight months since sowing, is short and results should therefore be viewed as preliminary in terms of understanding seedling emergence and the ecological dynamics of restoration.

3. Results

3.1. Responses to seeding

The effect of seeding on overall indigenous plant and seedling density, species richness and canopy cover indicated that seeding contributed significantly to all three criteria: density ($\chi^2 = 8.116$, $p = 0.004$), richness ($\chi^2 = 19.23$, p = <0.001) and canopy cover ($\chi^2 = 4.258$, p = 0.039). Seeding increased overall indigenous density by approximately 18%, richness by approximately 30% and cover by approximately 18%. Seeding also had a significant positive effect on existing indigenous species richness (F = 4.77, p = 0.031) (Tables 4 and 5).

3.2. Intervention responses

At the main-factor level, the application of herbicide resulted in significant positive effects on all criteria of the seeded species (seedling density, species richness, canopy cover and seedling height) and significantly promoted richness and cover of the existing indigenous species whilst significantly inhibiting weed canopy cover. Burning significantly promoted all aspects of the existing indigenous species and significantly reduced weed cover but also significantly reduced the density and richness of the sown species. Tillage significantly promoted density, richness and canopy cover of both the seeded and existing indigenous species. Rodent-exclusion significantly reduced the density and canopy cover of the seeded species and the density of existing indigenous species yet significantly promoted weed cover. Seeding had a significant positive effect on the richness of existing indigenous species. A summary of the main and interaction effect sizes is presented in Table 5.

Due to the numerous interventions and response variables, the results below do not report statistical values. For chi squared (χ^2), variance ratio (F) and probability values refer to Table 4. For response direction, median and inter-quartile range refer to Table 5 (refer to Table 1 for acronyms).

3.3. Seeded species

3.3.1. Seeded species: seedling density

Significant positive effects on density of seeded species resulted from S, TS, HS, THS, HRS, BTRS, and BTHRS whilst significant negative effects resulted from BS and RS.

Considering untransformed median values, S implemented individually (without another intervention) resulted in the lowest seedling density (6.5 seedlings per m^2). Of the two-factor interventions (S plus another intervention) the density was highest in response to TS (91.8 seedlings per m^2) followed by HS (64.0 seedlings per m^2). The following three- to five-factor interventions resulted in greater seedling density than TS, in ascending order: BTHRS, BTHS, THRS and THS which resulted in 169.3 seedlings per m^2.

3.3.2. Seeded species: species richness

Significant positive effects with respect to species richness resulted from S, TS, HS, BTS, THS, HRS and BTHRS whilst a significant negative effect resulted from BS.

The seeding-only treatment resulted in the lowest species richness (1.3 species per m^2) with TS and HS both resulting in 5.0 species per m^2 (the highest of the two-factor interventions). All of the remaining three- to five-factor interventions, with the exception of BRS, resulted in species richness equal to or higher than TS and HS. THRS resulted in the highest richness with 7 species per m^2.

3.3.3. Seeded species: canopy cover

The interventions S, TS, HS, THS and TRS resulted in significant positive effects on seeded species canopy cover whilst RS resulted in a significant negative effect.

Seedling canopy cover was lowest when only S was implemented (0.5% canopy cover). Of the two-factor interventions HS resulted in the highest cover (5.8% canopy cover). Among the three- to five-factor interventions, canopy cover for HS was exceeded by six interventions, in ascending order: BHS, BHRS, THS, THRS, and, BTHS and BTHRS both resulting in the highest canopy cover of 9%.

3.3.4. Seeded species: seedling height

Significant positive effects on seedling height of the seeded species resulted from S, HS, THS, BRS and BTRS.

Seedling height was lowest in the S-only plots with a median seedling height of 3.8 cm. Among the two-factor interventions, median seedling height was greatest in HS (8.6 cm). Of the three- to five-factor interventions, seedling height for HS was exceeded by six interventions, in ascending order: BRS, BTHS, THRS, HRS, BHS and BTHRS (12.8 cm).

3.3.5. Seeded species: seedling survival

Just over a quarter (25.8%) of the total number of seedlings recorded in September 2012 survived to the January 2013 census. What appears to be nearly a 75% seedling mortality rate was largely due to the high proportion of deciduous geophytes which in September 2012 comprised 72.04% of the total number of individuals.

The highest number of geophytes is recorded in September 2012 and due to dormancy, above-ground presence drops to 0.5% by January 2012. The succulent shrub survival rate is relatively low at 12.5%. Graminoid density tapers off slightly in January 2013 but maintains a 54.3% survival rate. Tall shrubs and low shrubs have the highest survival rates at 73.6% and 75.3% respectively.

The median number of sown seedlings per m^2 per intervention over the four data collections is provided in Fig. 2.

Responses among species were highly varied, ranging, for instance, from 8981 *Ornithogalum thyrsoides* seedlings per 96 m^2 to one *Searsia tomentosa* seedling per 96 m^2.

3.4. Existing indigenous species

3.4.1. Existing indigenous species: seedling density

Significant positive effects on seedling density of existing indigenous species resulted from B, T and BH. Significant negative effects resulted from R and HR.

The control resulted in the lowest density with 146.5 plants per m^2. Of the single-factor interventions, B resulted in the highest density (286.0 plants per m^2) and T thereafter with 265.3 plants per m^2. Of the two- to four-factor unseeded interventions, four interventions result in a density greater than B and each contains the factors B and T: BTH, BTR and BTHR (each with 315.5 plants per m^2) and BT with 350.8 plants per m^2. Of the seeded interventions, the factors B and T similarly contribute to good performance of existing indigenous species and BTS resulted in the highest density of 313.0 plants per m^2.

3.4.2. Existing indigenous species: species richness

Significant positive effects on existing indigenous species richness resulted from S, B, T, H and BTH. With the exception of R, which had a negative effect, the remaining interventions resulted in non-significant positive effects.

The lowest species richness was recorded in the control (3.0 species per m^2). Of the single-factor interventions, B and T resulted in the highest richness (6.0 species per m^2). Of the unseeded interventions, all of the two- to four-factor interventions resulted in species richness equal to or higher than B and T, the highest being BT, BTH, BTR, BHR, and BTHR, each resulting in 7.0 species per m^2. Considering the two- to five-factor seeded interventions, the following achieved richness equal to or more than 7.0 species per m^2, in ascending order: BTS, BHS, BRS, BTHS, BTRS, BHRS, THRS and the highest, BTHRS, with 8.0 species per m^2.

3.4.3. Existing indigenous species: canopy cover

The interventions B, T and H resulted in significant positive effects with respect to canopy cover for existing indigenous species.

Seeding-only resulted in the lowest cover of 15.1%. Of the single-factor interventions, H resulted in the highest canopy cover with 23.3%. The two-factor interventions exceeding H include: TR, BR, BH and HR with 31.8% cover. Of the three- to five factor interventions,

Table 5
Summary statistics for the 16 seeded and 16 unseeded interventions including the untransformed medians (lower quartile, upper quartile) when all factors of the intervention are not implemented (0) and when all factors of the intervention are implemented (1), and the resultant response direction (+ve, −ve). The median calculations for each intervention disregard the other factors not included in the intervention as the data is pooled across all levels of the other factors.

		Seeded interventions							
		Seeded species				Existing indigenous species			Weed species
		Density Median no. seedlings per m^2 (Jul 2012, Sep 2012, Nov 2012, Jan 2013)	Richness Median no. species per m^2 (Jul 2012, Sep 2012, Nov 2012, Jan 2013)	Cover Median % cover per m^2 (Sep 2012, Nov 2012, Jan 2013)	Height Median seedling height per m^2 (Sep 2012, Nov 2012, Jan 2013)	Density Median no. plants per m^2 (Sep 2012)	Richness Median no. species per m^2 (Sep 2012)	Cover Median % cover per m^2 (Sep 2012, Nov 2012, Jan 2013)	Cover Median % cover per m^2 (Nov 2012)
S	0	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)	206.5 (118.8, 292.8)	5.0 (3.0, 6.0)	19.0 (4.4, 46.6)	92.0 (73.9, 100.0)
	1	6.5 (0.9, 18.6)	1.3 (0.5, 6.6)	0.5 (0, 1.3)	3.8 (2.6, 5.3)	205.5 (127.9, 274.6)	5.8 (4.0, 7.0)	15.1 (4.2, 37.0)	95.0 (79.8, 100.0)
		+ ve	+ ve	+ ve	+ ve	− ve	+ ve	− ve	+ ve
BS	0	40.8 (8.4, 193.6)	4.5 (2.0, 7.0)	3.0 (0.8, 6.5)	5.9 (3.9, 9.7)	118.5 (85.8, 203.9)	3.8 (3.0, 5.1)	16.8 (5.9, 41.0)	96.5 (81.8, 100.0)
	1	34.5 (6.0, 90.0)	3.5 (1.5, 5.0)	3.3 (0.7, 6.6)	7.5 (3.6, 12.8)	264.8 (211.8, 333.0)	6.8 (5.4, 7.0)	15.8 (5.0, 56.0)	92.5 (72.0, 100.0)
		− ve	− ve	+ ve	+ ve	+ ve	+ ve	− ve	− ve
TS	0	9.0 (1.0, 37.9)	2.0 (0.5, 4.0)	1.0 (0.0, 4.0)	6.1 (4.3, 15.2)	156.5 (105.0, 218.0)	4.0 (2.9, 5.0)	18.8 (2.0, 42.3)	95.8 (71.0, 100.0)
	1	91.8 (39.6, 239.5)	5.0 (3.5, 8.0)	5.0 (2.9, 8.3)	6.5 (3.4, 9.5)	262.5 (179.4, 332.25)	6.0 (5.0, 7.0)	17.0 (5.0, 40.0)	94.5 (85.3, 100.0)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	− ve	− ve
HS	0	11.3 (0.5, 68.6)	2.0 (0.5, 5.0)	1.0 (0.0, 3.1)	4.6 (2.8, 7.5)	225.5 (133.6, 329.8)	4.8 (3.0, 6.0)	13.3 (2.4, 41.3)	100.0 (99.5, 100.0)
	1	64.0 (30.0, 188.3)	5.0 (3.0, 7.0)	5.8 (3.0, 11.8)	8.6 (4.9, 15.5)	211.3 (148.0, 263.4)	6.0 (4.5, 7.0)	20.0 (7.6, 42.8)	81.0 (59.8, 94.3)
		+ ve	+ ve	+ ve	+ ve	− ve	+ ve	+ ve	− ve
RS	0	47.0 (11.3, 164.6)	3.5 (1.9, 6.0)	3.9 (1.0, 7.0)	6.2 (3.2, 10.2)	223.75 (150.8, 318.5)	5.5 (3.9, 6.1)	16.3 (3.9, 43.6)	79.5 (60.6, 99.5)
	1	26.5 (5.5, 96.3)	4.0 (2.0, 6.0)	3.0 (0.5, 5.6)	7.3 (4.2, 10.3)	191.5 (123.0, 261.3)	6.0 (4.0, 7.0)	19.5 (5.0, 40.3)	100.0 (93.8, 100.0)
		− ve	+ ve	− ve	+ ve	− ve	+ ve	+ ve	+ ve
BTS	0	10.5 (1.0, 44.3)	2.5 (0.5, 4.6)	1.0 (0.0, 3.5)	5.6 (4.5, 11.3)	105.0 (70.5, 119.4)	3.0 (2.0, 3.6)	19.0 (5.5, 36.0)	95.3 (59.5, 100.0)
	1	77.8 (38.9, 178.4)	5.0 (3.0, 6.0)	4.8 (2.5, 8.8)	7.5 (3.4, 10.0)	313.0 (269.4, 376.0)	7.0 (5.8, 8.0)	16.4 (5.5, 64.0)	89.8 (74.6, 95.8)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	− ve	− ve
BHS	0	12.0 (0.9, 95.8)	2.8 (0.5, 7.0)	1.1 (0.0, 3.8)	4.8 (2.8, 6.1)	129.3 (80.3, 180.8)	3.0 (2.0, 4.3)	8.5 (2.8, 31.5)	100.0 (99.9, 100.0)
	1	60.0 (31.0, 178.4)	5.0 (3.0, 6.0)	6.5 (4.0, 12.8)	10.1 (4.6, 17.9)	252.0 (211.8, 291.1)	7.0 (5.9, 7.3)	25.5 (10.5, 63.5)	71.0 (35.4, 89.6)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	− ve
THS	0	1.0 (0.0, 4.9)	0.5 (0.0, 1.6)	0.0 (0.0, 0.5)	3.0 (2.6, 5.0)	156.5 (120.1, 295.6)	3.5 (2.0, 5.0)	8.0 (1.2, 31.5)	100.0 (100.0, 100.0)
	1	169.3 (56.1, 277.6)	6.3 (4.5, 8.0)	7.0 (4.7, 16.9)	8.5 (5.0, 11.6)	264.8 (203.4, 306.0)	6.0 (5.4, 7.3)	20.0 (11.4, 51.0)	91.3 (70.1, 97.8)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	− ve
BRS	0	47.0 (10.8, 239.1)	4.3 (2.4, 7.6)	3.9 (0.9, 7.0)	5.7 (3.9, 9.6)	146.5 (104.1, 216.4)	4.5 (3.0, 6.0)	16.3 (7.3, 36.7)	90.8 (73.3, 99.6)
	1	25.5 (3.8, 74.5)	4.0 (2.0, 5.3)	3.0 (0.5, 6.3)	7.8 (4.2, 17.7)	248.5 (197.0, 277.3)	7.0 (5.8, 8.0)	19.5 (4.5, 60.0)	96.5 (89.5, 100.0)
		− ve	− ve	− ve	+ ve	+ ve	+ ve	+ ve	+ ve
TRS	0	12.3 (1.5, 47.0)	2.5 (1.0, 4.0)	1.4 (0.3, 6.3)	5.5 (3.3, 13.2)	175.5 (119.5, 257.9)	4.0 (2.9, 6.0)	15.8 (1.9, 39.0)	90.3 (51.1, 100.0)
	1	82.5 (25.0, 204.3)	5.5 (4.0, 8.0)	4.8 (2.0, 10.5)	6.2 (4.0, 9.5)	261.5 (204.0, 306.0)	6.5 (5.8, 7.5)	22.8 (11.0, 51.0)	100.0 (95.0,100.0)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve
HRS	0	28.5 (1.4, 84.5)	2.8 (1.0, 5.0)	1.4 (0.3, 4.1)	5.5 (2.7, 7.7)	284.3 (205.3, 354.9)	5.3 (3.8, 6.5)	8.9 (3.1, 52.5)	99.5 (90.1, 100.0)
	1	61.5 (29.3, 175.8)	5.5 (4.0, 7.0)	5.3 (3.0, 10.8)	9.2 (5.7, 17.9)	214.5 (188.5, 270.5)	6.0 (4.5, 7.3)	26.5 (12.0, 51.0)	93.5 (82.0, 97.0)
		+ ve	+ ve	+ ve	+ ve	− ve	+ ve	+ ve	− ve
BTHS	0	1.0 (0.0, 9.3)	0.5 (0.0, 2.0)	0.0 (0.0, 0.5)	3.8 (2.6, 5.3)	119.8 (80.3, 142.3)	2.5 (2.0, 3.3)	11.3 (1.9, 31.5)	100.0 (100.0, 100.0)
	1	124.3 (56.1, 195.0)	5.3 (4.5, 7.0)	9.0 (5.2, 14.9)	8.9 (4.0, 16.6)	293.8 (266.1, 340.8)	7.0 (6.5, 8.3)	17.5 (11.4, 64.3)	72.8 (54.6, 94.3)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	− ve
BTRS	0	14.5 (2.6, 51.9)	2.5 (1.0, 4.1)	1.3 (0.5, 6.4)	5.5 (4.5, 13.7)	118.5 (104.1, 142.3)	3.0 (2.4, 3.6)	17.5 (6.5, 35.4)	80.8 (51.1, 100.0)
	1	60.5 (13.5, 141.3)	5.0 (3.8, 6.3)	4.3 (2.0, 8.8)	7.6 (4.0, 14.6)	284.5 (261.8, 332.3)	7.0 (6.5, 9.0)	25.0 (11.0, 69.3)	96.5 (94.8, 100.0)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve
BHRS	0	19.0 (1.5, 68.6)	3.0 (1.0, 7.0)	1.4 (0.4, 4.1)	5.4 (2.7, 6.4)	188.5 (133.6, 254.5)	4.5 (2.8, 6.0)	11.6 (4.4, 43.9)	99.8 (95.8, 100.0)
	1	65.5 (39.3, 141.3)	5.0 (4.0, 7.0)	6.5 (4.0, 11.8)	16.4 (6.0, 21.6)	252.0 (212.5, 271.3)	7.0 (6.8, 8.3)	40.0 (11.0, 73.5)	86.0 (63.8, 94.3)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	− ve
THRS	0	1.5 (0.0, 11.6)	1.0 (0.0, 2.1)	0.3 (0.0, 0.8)	2.8 (2.4, 4.8)	268.3 (150.8, 318.5)	4.3 (2.4, 5.3)	10.0 (1.1, 52.6)	100.0 (99.9, 100.0)
	1	125.5 (72.5, 269.8)	7.0 (5.0, 9.0)	7.8 (5.4, 19.4)	8.9 (5.9, 16.6)	279.0 (249.5, 306.0)	7.0 (6.0, 9.0)	31.5 (17.8, 54.8)	97.5 (93.3, 100.0)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	− ve
BTHRS	0	6.5 (0.9, 18.6)	1.3 (0.5, 2.6)	0.5 (0.0, 1.3)	3.8 (2.6, 5.3)	146.5 (133.6, 178.1)	3.0 (2.0, 4.5)	19.5 (5.3, 45.9)	100.0 (99.9, 100.0)

	1	112.5 (72.5, 195.0)	6.5 (5.0, 7.3)	9.0 (5.9, 14.1)	12.8 (5.5, 18.8)	280.5 (261.8, 306.0)	8.0 (7.0, 9.3)	35.0 (13.5, 65.6)	94.5 (79.5, 96.3)
		+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	+ ve	− ve

Unseeded interventions

		Seeded species				Existing indigenous species			Weed species
		Density	Richness	Cover	Height	Density	Richness	Cover	Cover
		Median no. seedlings per m^2 (Jul 2012, Sep 2012, Nov 2012, Jan 2013)	Median no. species per m^2 (Jul 2012, Sep 2012, Nov 2012, Jan 2013)	Median % cover per m^2 (Sep 2012, Nov 2012, Jan 2013)	Median seedling height per m^2 (Sep 2012, Nov 2012, Jan 2013)	Median no. plants per m^2 (Sep 2012)	Median no. species per m^2 (Sep 2012)	Median % cover per m^2 (Sep 2012, Nov 2012, Jan 2013)	Median % cover per m^2 (Nov 2012)
C	1					146.5 (133.6, 178.1)	3.0 (2.0, 4.5)	19.5 (5.3, 45.9)	100 (99.9, 100)
B	0					127.3 (82.5, 199.4)	4.0 (3.0, 5.6)	15.4 (4.5, 32.8)	96.5 (85.3, 100.0)
	1					286.0 (212.8, 358.8)	6.0 (5.0, 7.0)	18.8 (3.9, 57.6)	89.8 (69.4, 100.0)
						+ ve	+ ve	+ ve	− ve
T	0					150.0 (105.0, 213.3)	4.0 (3.0, 6.0)	15.1 (2.0, 37.9)	95.8 (73.8, 100.0)
	1					265.3 (192.4, 354.4)	6.0 (5.0, 7.0)	17.8 (5.4, 50.3)	93.0 (77.9, 100.0)
						+ ve	+ ve	+ ve	− ve
H	0					196.8 (120.1, 324.5)	5.0 (3.0,6.1)	9.4 (2.0, 34.1)	100.0 (97.5, 100.0)
	1					208.0 (140.5, 263.4)	5.5 (4.0, 7.0)	23.3 (9.4, 46.6)	77.5 (51.9, 91.6)
						+ ve	+ ve	+ ve	− ve
R	0					218.8 (143.9, 317.5)	5.5 (4.0, 6.5)	14.0 (3.9, 34.6)	86.8 (67.3, 98.5)
	1					197.5 (116.3, 261.3)	5.0 (3.0, 7.0)	20.0 (5.0, 48.0)	100.0 (91.0, 100.0)
						− ve	− ve	+ ve	+ ve
BT	0					105.0 (70.5, 126.6)	3.0 (2.5, 4.0)	15.0 (4.0, 32.1)	95.8 (79.5, 100.0)
	1					350.8 (287.3, 410.5)	7.0 (5.5, 8.0)	21.8 (5.9, 69.8)	86.8 (67.8, 95.8)
						+ ve	+ ve	+ ve	− ve
BH	0					123.3 (72.8, 170.3)	4.0 (3.0, 5.0)	9.0 (2.9, 24.1)	100.0 (98.5, 100.0)
	1					252.0 (211.0, 309.8)	6.8 (5.4, 7.3)	28.0 (10.4, 66.0)	69.3 (40.9, 82.0)
						+ ve	+ ve	+ ve	− ve
TH	0					142.0 (107.8, 257.9)	4.0 (3.0, 5.0)	8.5 (1.0, 28.1)	100.0 (100.0, 100.0)
	1					264.8 (204.6, 334.5)	6.0 (5.0, 7.0)	22.0 (10.8, 53.3)	81.5 (67.8, 95.5)
						+ ve	+ ve	+ ve	− ve
BR	0					143.3 (104.1, 205.3)	4.3 (3.0, 6.0)	13.5 (4.5, 29.7)	91.3 (75.4, 98.5)
	1					248.5 (201.8, 332.3)	6.5 (5.0, 8.0)	24.0 (5.8, 66.5)	96.5 (78.5, 100.0)
						+ ve	+ ve	+ ve	+ ve
TR	0					182.8 (199.8, 244.5)	4.0 (3.0, 6.0)	15.0 (1.7, 34.6)	92.0 (51.1, 100.0)
	1					257.5 (176.8, 332.3)	6.0 (5.0, 7.0)	23.8 (8.0, 60.8)	100.0 (94.8, 100.0)
						+ ve	+ ve	+ ve	+ ve
HR	0					277.5 (151.8, 336.8)	5.0 (4.0, 6.6)	7.5 (2.7, 38.1)	98.5 (90.5, 100.0)
	1					212.0 (140.3, 270.5)	6.0 (4.0, 7.0)	31.8 (10.9, 57.0)	91.0 (76.3, 95.3)
						− ve	+ ve	+ ve	− ve
BTH	0					104.0 (72.0, 135.0)	3.0 (2.4, 4.0)	12.3 (1.9, 26.3)	100.0 (100.0, 100.0)
	1					315.5 (287.3, 372.6)	7.0 (5.4, 8.0)	25.0 (11.0, 73.1)	66.5 (45.4, 86.8)
						+ ve	+ ve	+ ve	− ve
BTR	0					119.0 (97.6, 139.0)	3.3 (2.9, 4.0)	15.1 (5.4, 32.6)	89.3 (57.9, 100.0)
	1					315.5 (268.0, 283.5)	7.0 (6.0, 8.3)	30.0 (12.4, 73.5)	96.5 (90.3, 100.0)
						+ ve	+ ve	+ ve	+ ve
BHR	0					148.5 (114.8, 240.4)	4.0 (3.0, 5.3)	9.4 (3.2, 23.5)	98.5 (95.4, 100.0)
	1					252.0 (211.0, 309.8)	7.0 (6.0, 8.3)	41.5 (11.6, 74.6)	78.0 (57.0, 92.3)
						+ ve	+ ve	+ ve	− ve
THR	0					245.5 (135.0, 324.5)	4.0 (2.9, 5.3)	6.8 (1.0, 38.8)	100.0 (99.9, 100.0)
	1					279.0 (214.3, 336.3)	6.5 (5.8, 7.3)	33.5 (16.3, 64.5)	94.5 (89.5, 100.0)
						+ ve	+ ve	+ ve	− ve
BTHR	0					132.0 (111.9, 145.3)	3.5 (2.4, 4.3)	13.5 (4.5, 32.1)	100.0 (99.3, 100.0)
	1					315.5 (289.8, 376.0)	7.0 (7.0, 8.3)	48.0 (17.0, 74.6)	88.5 (57.0, 94.3)
						+ ve	+ ve	+ ve	− ve

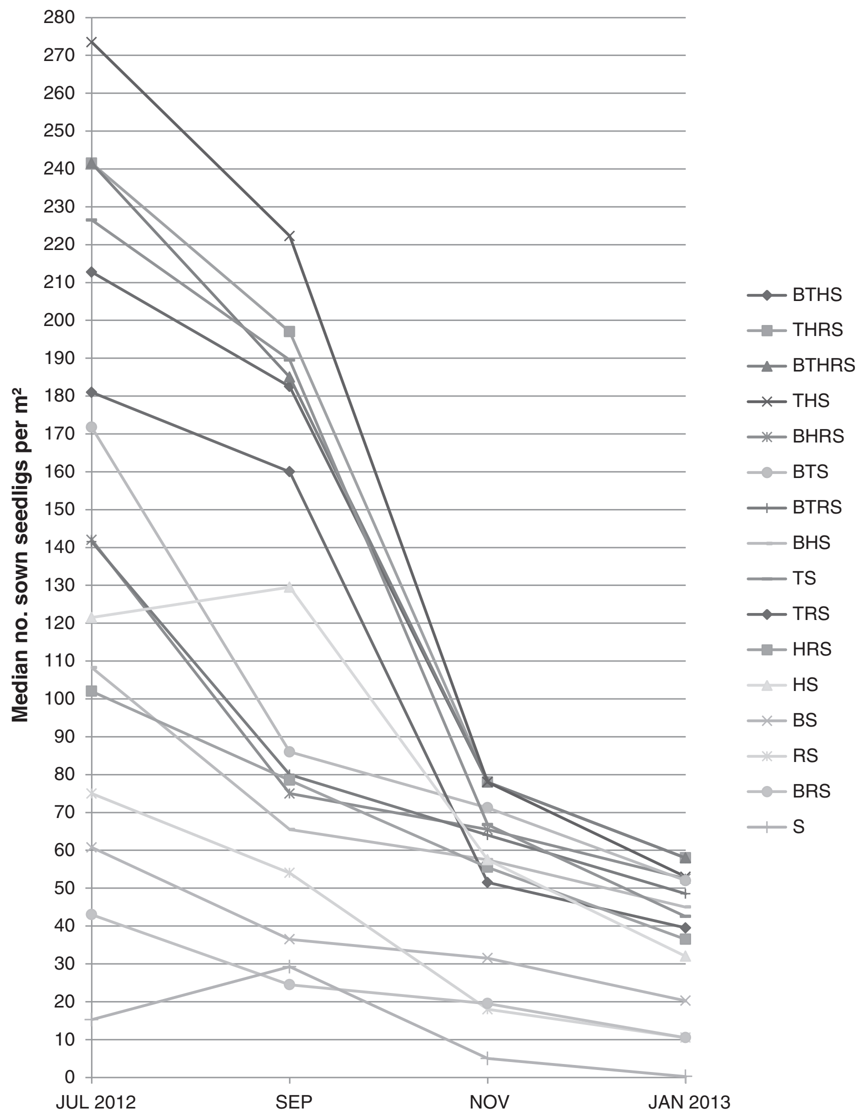

Fig. 2. The median number of sown seedlings per m^2 per intervention over the four data collections.

five interventions resulted in higher canopy cover than HR, in ascending order: THR, BTHRS, BHRS, BHR and BTHR with 48% cover.

3.5. Weed species: canopy cover

Significant positive effects, i.e. interventions promoting weed canopy cover, resulted from R and TR. Significant negative effects, i.e. interventions inhibiting weed cover, resulted from B, H, BT, BH and TH.

Median canopy cover of the control plots was 100% cover. Across both seeded and unseeded interventions, the most effective single-factor intervention in suppressing weed cover was H (77.5% cover). Of the two-factor interventions, BH resulted in lower weed cover than H, with 69.3% cover. Of the remaining three- to five-factor interventions, BTH was the most effective, reducing cover to 66.5%.

3.6. Vegetation structure

Fig. 3a–c illustrate the median percentage canopy cover per m^2 for each of the 16 seeded interventions for September 2012, November 2012 and January 2013 with respect to seeded species, existing indigenous species and weed species whilst Fig. 4a–c illustrate the breakdown of the seeded species per growth form (graminoids, geophytes, forbs, succulent shrubs, low shrubs and tall shrubs).

3.6.1. Canopy cover: seeded species, existing indigenous species and weed species

In general weed species cover peaked in November 2012 and declined dramatically in January 2013 due to the weed species being predominantly alien, annual grasses. The existing indigenous species cover was greatest in September 2012, declined dramatically in November 2012 and declined further in January 2013. With the exception of one perennial existing indigenous species (*Senecio pubigerus*) which increased in cover considerably from November 2012 to January 2013, the bulk of the existing indigenous species, being ephemeral geophytes, were largely dormant by the November 2012 census. The seeded species component contributed a very small proportion of the canopy cover make-up in September 2012, increasing in November 2012 and again notably in January 2013 where it contributed over half of the canopy cover of the total living biomass for some interventions, despite the forb and geophytic growth forms of the seeded species being almost absent above-ground in the January 2013 census.

3.6.2. Canopy cover: growth form breakdown within the seeded species

Increased cover in January 2013 can largely be attributed to increased cover in the low-shrub growth-form category and to lesser extents in the graminoid and large-shrub categories. All six growth forms were represented in the September 2012 census with a maximum of

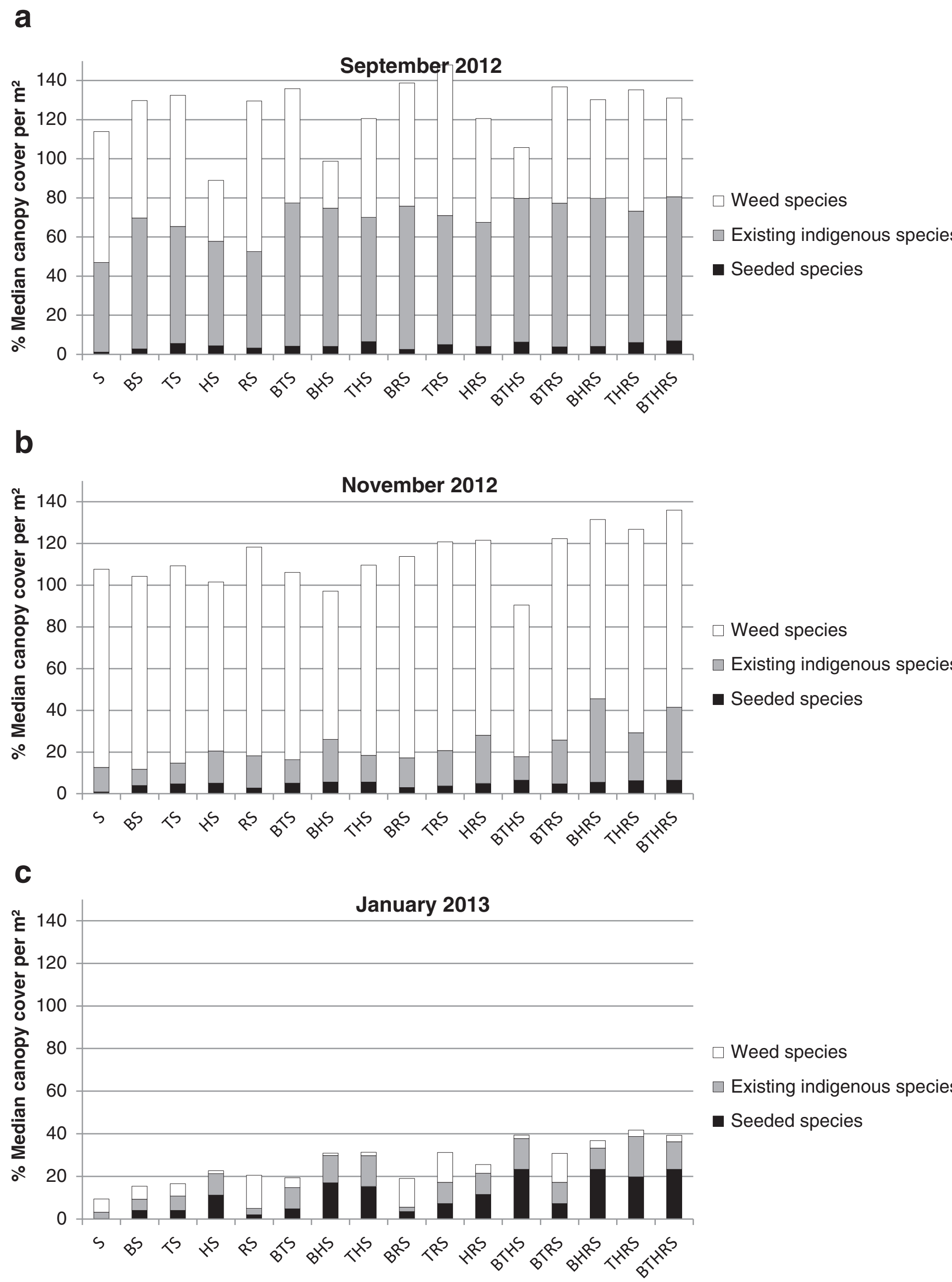

Fig. 3. a–c: Median percentage canopy cover per m^2 for each of the 16 seeded interventions for September 2012, November 2012 and January 2013 with respect to seeded species, existing indigenous species and weed species.

five growth forms being represented in several interventions (Fig. 4a). By November 2012 and January 2013, both the forb and succulent shrub growth forms dropped away and a maximum of four growth forms were plotted for several interventions: low and tall shrubs, graminoids and geophytes, the latter largely occurred within the rodent-exclusion plots most likely due to low light conditions (Fig. 4b and c).

4. Discussion

4.1. Seeding

There is a large body of literature documenting a wide range of restoration outcomes from projects failing to achieve adequate seedling emergence (Holmes, 2002; Midoko-Iponga, 2004; Pausas et al., 2004; deFalco et al., 2012; Heelemann, 2012; Vallejo et al., 2012) to projects achieving higher levels of emergence and thus contributing to the attainment of desirable ecosystem attributes, including species richness, community structure and function (Jones and Hayes, 1999; Allen et al., 2000; Holmes, 2001, 2005; Joubert et al., 2009; Vallejo et al., 2009). Responses to the interventions in this study were similarly variable with seedling recruitment ranging from poor to very good.

Whether attributing seedling germination and establishment to the lottery model (Warner and Chesson, 1985) or to the competition/colonisation trade-off (Tilman, 1994) models of seed limitation, recruitment following species introduction by sowing affirms the existence of the regeneration niche and as a result implicates dispersal limitation as a factor resulting in the absence of species (Turnbull et al., 2000). In this study, recruitment in the seeding-only plots confirmed

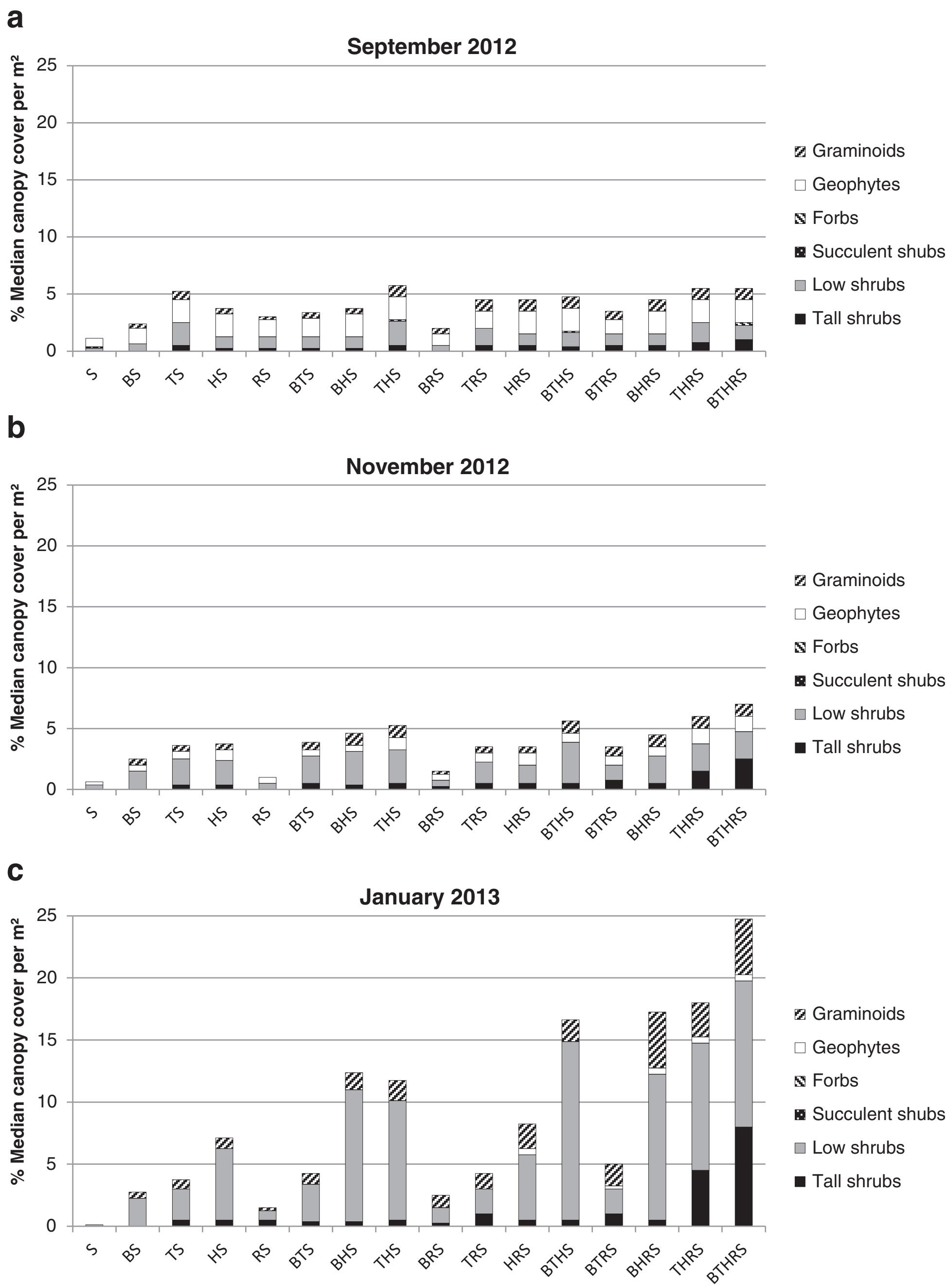

Fig. 4. a–c: Median percentage canopy cover per m^2 of the seeded species per growth form for September 2012, November 2012 and January 2013.

that a lack of seed reaching the area was a barrier to community recovery.

Seeding had profoundly positive effects with respect to all of the seeded species criteria. Seeding made a dramatic contribution to overall indigenous community attributes in an otherwise depauperate, geophytic community, emphasising the valuable role of seed augmentation in ecological restoration, a recognised limitation world-wide (Holmes and Richardson, 1999; Turnbull et al., 2000; Holmes, 2002, 2005, 2008; Pywell et al., 2002, 2003; Del Moral et al., 2007; Standish et al., 2007; Memiaghe, 2008; Clewell and Aronson, 2013).

The infestation of alien, annual grasses suppressed seedling recruitment, consistent with other seed-based renosterveld restoration studies (Holmes, 2002; Midoko-Iponga, 2004) and numerous Mediterranean-climate ecosystem studies (Eliason and Allen, 1998; Stylinski and Allen, 2001; Standish et al., 2007; Beyers, 2009). The seeding-only intervention resulted in the lowest performances with respect to all of the seeded species criteria and recruitment dramatically improved for all criteria when implemented in combination with one or more of the other interventions which functioned to reduce weed cover. This finding is consistent with the Holmes (2005) study which found that the implementation of seeding-only, without another intervention to reduce weed cover, resulted in poorer recruitment. The underlying mechanism of such dynamics evident in this study is most likely the reduction in weed cover, and thus an increase in the availability of microsites and a reduction in competition, achieved by the two- to five-factor interventions facilitating enhanced recruitment. This indicates that dispersal limitation was not the only factor inhibiting species colonisation but that alien grasses played a large role in reducing available colonisation sites and exerting competitive pressure.

Median seedling density per m^2 notably exceeded density in similar seed-based restoration studies (Holmes, 2002, 2005). In the two year trial period of the Holmes (2002) study, non-significant differences between the seeded and unseeded plots were recorded and at the first six month census there was an average of five seedlings per m^2. Seedling density was notably higher in the Holmes (2005) study with an average of 80 seedlings per m^2 in the ploughed plots, but declined dramatically after the first summer measuring five seedlings per m^2 within three years. There are numerous variables making comparisons difficult yet the difference in seedling densities can most likely be attributed principally to the variation in soil preparation treatments. In addition to soil preparation variables, the difference in seed-sowing rates likely also contributes to the disparity: in the Holmes (2002) study, Holmes (2005) study and this study, respective rates sown were 50 kg uncleaned seed, 300 kg uncleaned seed and approximately 57 kg semi-cleaned seed per hectare.

To gain insight into how seedling density and richness of the restored plots from this study compare with natural renosterveld vegetation, findings were compared with burnt remnants of Swartland Shale Renosterveld in Tygerberg Nature Reserve. The analysis revealed that the restored plots had almost two and a half times the density of indigenous seedlings and plants as the natural vegetation. This can in part be attributed to a high abundance of *Oxalis* seedlings in this study which were generally slender and clumped *en masse*. Additional factors possibly responsible for the discrepancy in density include the levels of granivory and/or herbivory and the soil-preparation techniques implemented in this study. The same data sets were compared with respect to indigenous species richness per m^2, and in this study, overall indigenous species richness was just over 56% of that in the Tygerberg plots, attributable in part to the limited number of species selected for reintroduction.

The significant positive effect seeding had on existing indigenous species richness is difficult to explain but may have resulted from a shift in species interactions that promoted some suppressed, existing species.

4.2. Burning

Burning stimulated recruitment and increased performance of all criteria of the existing indigenous species, in keeping with studies in fire-driven ecosystems elsewhere (Keeley, 1991; Hester and Hobbs, 1992; Allen et al., 2000; Bell, 2001; Safford and Harrison, 2004) and in the fynbos biome (Holmes and Richardson, 1999; Midoko-Iponga, 2004; Musil et al., 2005; Rebelo et al., 2006; Milton, 2007; Curtis, 2013).

Of concern are the findings that both density and richness of the seeded species were significantly inhibited in the burnt plots. These results were unexpected as post-fire conditions of high levels of nutrients (Brown and Mitchell, 1986; Stock and Lewis, 1986; Musil and Midgley, 1990), light and water generally promote seedling emergence (Bond and Van Wilgen, 1996). The burn significantly reduced weed cover yet promoted the existing indigenous species and it is possible that the net effect may have increased levels of resource competition exerted on the seeded species. The leachate of the dominant annual alien grass species, *A. fatua*, has been shown to have an allelopathic effect on seed germination (Tinnin and Muller, 1972) and the ash of this species may have acted as a germination suppressant. As all of the seed used in this experiment, for both the unburnt and burnt plots, was smoke-treated prior to sowing, it suggests the role of an environmental variable/s rendering the burnt plots less suitable for recruitment. Further to fire resulting in a flush of nutrients (lasting four and nine months for phosphorus and nitrogen respectively (Allsopp and Stock, 1992)), fire has been found to reduce the propagule density of vesicular–arbuscular mycorrhiza and thus the level of seedling infectivity (Klopatek et al., 1988; Vilarino and Arines, 1991; Allsopp and Stock, 1995). Mycorrhizal infection in seedlings occurs in the majority of species (Fenner and Thompson, 2005) and is likely critical for healthy seedling development as soil phosphorus uptake in non-mycorrhizal seedlings has been shown to be inhibited (Allsopp and Stock, 1995). Renosterveld vegetation has high levels of infectivity (Allsopp and Stock, 1994); however, it is unlikely that the quick autumn fire in this study resulted in soil temperatures high enough to affect propagule density. Intense fires in fynbos have been found to cause soil water repellency (Scott and Van Wyk, 1992; Bond and Van Wilgen, 1996) but again, the characteristics of the on-site fire make this unlikely. Increased levels of rodent granivory and/or herbivory in a post-fire environment (Bond, 1984) can in this instance be discounted as seedling density was lower inside the cages than outside. The many inhibitive effects of dense leaf litter on seedling emergence and establishment are widely reported (Facelli and Pickett, 1991; Facelli, 1994; Lenz et al., 2003) yet, in this study, the net effect of conditions in the unburnt plot (whether merely less inhibitive or possibly even facilitative) resulted in greater seedling recruitment than in the burnt plots. Midoko-Iponga (2004) hypothesised that grass litter, albeit the result of herbicide application, provided a mulching effect which increased soil moisture retention and resulted in higher seedling emergence. In this study, due to greater exposure to sunlight and wind, the soil in the burnt site may have retained moisture for shorter periods than the unburnt site which most likely experienced less moisture variability due to the shading effect of the leaf litter layer. The relatively exposed soil surface and greater moisture fluctuations in the burnt site, may have resulted in lower seedling emergence.

Burning significantly reduced weed cover. Controlling invasions of annual grasses with fire has been achieved to some extent particularly where fires are carefully timed to intercept grass seed set (Allen et al., 2000; D'Antonio and Meyerson, 2002; Midoko-Iponga, 2004; Keeley, 2006). However, in fire-driven Mediterranean-climate ecosystems in general, fire has been found to more commonly promote than inhibit invasive grasses (Minnich and Dezzani, 1998; Van Rooyen, 2003; Milton, 2004; Musil et al., 2005; Keeley, 2006; Memiaghe, 2008). The control of alien, annual grass by fire is likely a temporary response, as depending on the species involved and seed longevity, alien grass occurrence may return to pre-fire levels (Brooks and Pyke, 2001; Keeley, 2006) making the post-fire application of herbicide necessary. These findings emphasise the importance of long-term monitoring to determine the case-specific effect of fire on the weed species over time. It is furthermore possible that the promotion of the existing indigenous species by the burn may have exerted competitive pressure on the weed component.

4.3. Tillage

Tillage resulted in positive responses for all seeded and existing species criteria. The reduction in weed cover, created safe sites for seed germination and reduced grass-induced competition, and is most likely the driver of these significant positive effects. These responses are consistent with numerous seed-based studies where seedling establishment increases with cultivation-type disturbance (Turnbull et al., 2000; Holmes and Foden, 2001; Holmes, 2005; Joubert et al., 2009; deFalco et al., 2012). In renosterveld, small bulbils from geophytes (for example *Oxalis* species) are dispersed short distances in response to small and large mammal activity and ploughing (Shiponeni, 2003; Walton, 2006). In this study, since the majority of the existing indigenous species on site were geophytes, it is likely that their performance was promoted in part by the dispersal action of the tillage.

Although weed cover was apparently inhibited by tillage by the end of this study, it is possible that this result would give way with time as invasive, annual grasses are commonly found to increase with disturbance (Dowling, 1996; Allen et al., 2000; Stylinski and Allen, 2001; D'Antonio and Meyerson, 2002; Van Rooyen, 2003; Milton, 2004; Muhl, 2008; Sharma et al., 2010). In keeping with other interventions the transience of the positive effects of tillage possibly giving way to longer-term negatives show that successful long-term restoration requires on-going monitoring and management.

4.4. Herbicide application

The application of herbicide resulted in the desired outcomes with respect to all criteria. Numerous studies report successfully reducing alien species cover with the use of herbicide (Midoko-Iponga, 2004; Holmes, 2005, 2008; Musil et al., 2005; Cox and Allen, 2008; Memiaghe, 2008), yet, in keeping with other interventions such as burning and tillage, several report the temporary effectiveness of herbicide and follow-up treatment is widely advocated (Cione et al., 2002; Holmes, 2008; Standish et al., 2008). The competitive effect of alien, annual grasses has been shown both in-field and experimentally to have an inhibitory effect on renosterveld species (Midoko-Iponga et al., 2005; Musil et al., 2005; Muhl, 2008; Sharma et al., 2010) and in this study, the significant reduction in weed cover, and thus the reduction in competition, was most likely the driver of the high performances of both the seeded species and existing indigenous species. The reduction of these alien, annual grasses in other renosterveld studies has similarly been found to promote indigenous species performance (Midoko-Iponga, 2004; Musil et al., 2005). In addition to the positive ramifications of reduced grass competition, the removal of the above ground biomass of alien grasses, leaving the below ground root biomass to decay, has also been found to enhance the soil nutrient status (Campbell et al., 1991; Midoko-Iponga, 2004) and may have been a factor further promoting the performance of the indigenous species.

4.5. Rodent exclosure

During the eight month observation period, the level of seed and seedling consumption by rodents was evidently negligible on this site as seedling density of the seeded species was in fact lower inside the rodent-exclusion cages than outside. This finding may be in part explained by the small-mammal survey on Devil's Peak which found that the game camp supported the lowest rodent density of 102 individuals per hectare (compared with 206 individuals per hectare in old renosterveld stands), most likely due to the low structural diversity of the alien, annual grass and forb community (Dreyer, 2012). Generally, rodent densities are highest in autumn yet in the game camp the density was higher in spring (Dreyer, 2012). As the controlled burn was implemented in autumn, these population dynamics may reflect an initial decline in numbers associated with the fire followed by population recovery approximately six months later. These small-mammal population dynamics in response to fire are consistent with some, but not all, studies (Midgely and Clayton, 1990; Van Hensbergen et al., 1992; Bond and Van Wilgen, 1996).

The lower seedling and plant densities within the cages, with respect to both the seeded and existing indigenous species, may have resulted from the shading effect of the cages which were found to cut out approximately 55% of the light. These low light conditions may have reduced the maximum soil temperature affecting seed germination as has been found in other studies where low light affected germination and seedling emergence (Bond, 1984; Pausas et al., 2004; Castro et al., 2005).

The microclimate conditions within the cages favoured the weed species. The dominant invasive grass species, *A. fatua*, *B. maxima* and *B. minor*, are C3 grasses (Milton, 2004) having an affinity for low light conditions (Cowling, 1983). This very high weed cover would certainly have exerted competitive pressure on the seeded species and existing indigenous species.

4.6. Ecological-response model

Of the 40 predicted responses to the five main factors, as presented in the *a priori* model, half were confirmed by the experimental responses whilst half were unanticipated (Table 6). These unanticipated responses identify areas requiring further specific experimental work. Of the unexpected responses, 10 were beneficial to community attributes and 10 were detrimental. Some of the treatments that were successful in the span of this study are noted in the literature for promoting negative effects over time, making longer-term monitoring essential for increasing the accuracy and relevance of intervention effectiveness and the ecological-response model.

4.7. Intervention interactions

Of the 16 seeded interventions, seeding-only consistently performed the worst. When seeding was implemented in combination with another of the factors, the outcomes were vastly improved. Despite the notable merit of these two-factor interventions, none resulted in the desired responses for all of the measurement criteria due to downfalls in one or more of the performance areas. The intervention TS and HS are the best performing of the two-factor interventions in this regard but none the less each produced a non-significant adverse result, reducing the cover and density of existing species respectively. In contrast, six (of the 11) three- to five-factor seeded interventions (BHS, THS, BTHS, BHRS, THRS and BTHRS) produced the desired responses in all respects with positive responses for all of the seeded species and existing indigenous species criteria as well as having an inhibitive effect on weed cover. This view of enhancing intervention outcomes through the implementation of multiple factors *in lieu* of a single factor is supported locally by renosterveld and fynbos studies (Midoko-Iponga, 2004; Holmes, 2005; Midoko-Iponga et al., 2005; Musil et al., 2005; Memiaghe, 2008; Joubert et al., 2009) as well as international studies (Allen et al., 2000; Eliason and Allen, 1998; Pausas et al., 2004; Pywell et al., 2002; Standish et al., 2007; Standish et al., 2008).

5. Conclusions and recommendations

Through using experimental data to confirm or refute the *a priori* ecological-response model, this paper makes a theoretical contribution in developing the conceptual framework for restoration protocols in Peninsula Shale Renosterveld and potentially other similar renosterveld types.

- Seeding was imperative to shift the community to a shrubland state.
- Burning is recommended for the considerable positive effects it had on the existing indigenous community and the inhibitive effect on weed species.
- In old fields, tillage is recommended for the initial creation of safe-sites but requires implementation in conjunction with herbicide application.
- Herbicide application is highly recommended for the significant reduction in weed cover and for the positive responses exhibited by the seeded and existing indigenous species.
- Rodent exclusion is recommended but in an alternative form to the costly, light-intercepting cages used in this study. Alternative approaches, relatively cost-effective at scale, include the use of raptor perches to increase rodent predation (Milton, 2001; Holmes, 2002) and/or broadcasting chicken-feed seed mix to draw rodents away from the restoration site (Holmes, 2002).
- The ecological-response model was a useful means of considering standard ecological factors such as competition, disturbance, nutrients,

Table 6
Ecological-response model: summary explanations, actual experimental responses differing from predicted responses (framed).

INTERVENTION	SEEDED SPECIES	predicted	actual	EXISTING INDIGENOUS SPECIES	predicted	actual	WEED SPECIES	predicted	actual	
BURNING	Density	+	-*	Density	+	+***				Possibly due to allelopathic effect of grass ash, effects of diesel-petrol mix, increased exposure and lower moisture retention, and, increased competition from existing indigenous species.
	Richness	+	-***	Richness	+	+***				
	Cover	+	+	Cover	+	+*	Cover	+	-***	Potentially a short-term effect. Possibly due to increased competition from existing indigenous species.
	Height	+	+							
TILLAGE	Density	+	+***	Density	-	+***				Probably due to disturbance promoting the dispersal of *Oxalis* bulbils.
	Richness	+	+***	Richness	-	+***				Potentiallya short-term effect.Possibly due to increased competition from sown and existing indigenous species.
	Cover	+	+***	Cover	-	+*	Cover	+	-	
	Height	+	+							
HERBICIDE	Density	+	+***	Density	-	+				Possibly due to reduced competition with weeds.
	Richness	+	+***	Richness	-	+*				
	Cover	+	+***	Cover	-	+***	Cover	-	-***	
	Height	+	+***							Possibly due to alteration of micro-climate within cages e.g. low light, low soil temperature, wind protection.
RODENT-EXCLUSION	Density	+	-**	Density	0	-**				
	Richness	+	+	Richness	0	-				Probably due to low light conditions within cages promoting alien C3 grasses.
	Cover	+	-*	Cover	0	+	Cover	0	+***	
	Height	+	+							
SEEDING	Density	+	+***	Density	0	-				Difficult to explain. Negative responses possibly due to increased competition with seeded species and weed species. Both negative and positive responses possibly due to the untested effect of the seed-sand-fungicide mix. Could result from a shift in species interactions.
	Richness	+	+***	Richness	0	+*				
	Cover	+	+***	Cover	0	-	Cover	0	+	
	Height	+	+***							

Significant effects:* for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$.

dispersal, granivory and herbivory and provided a framework for thinking through the ecological aspects of why elements gave rise to certain outcomes. The model served to elucidate unexpected outcomes which can now inform further experimental work. For these reasons we recommend the use of such a model in future restoration studies.

Establishment of indigenous shrub cover has been found to successfully exclude invasive, annual grasses (Cione et al., 2002; Heelemann, 2012) and in this study some of the more successful interventions, achieving good cover of existing indigenous and seeded species, have the potential to suppress these grasses. The ability of the indigenous species component within each community to out-compete the alien, annual grass component over the longer-term is critical to future restoration outcomes. Long-term monitoring will be necessary to ascertain how the community develops with respect to composition, structure and function and in addition whether species complete life-cycles as a measure of how sustainable the restored community is (Holmes and Richardson, 1999). Assessing each of the interventions over the longer-term will reveal which communities, if any, ultimately suppress the alien annual grasses. This data will provide an accurate measure of intervention success, placing researchers and decision makers in a strong position with respect to how to proceed with the further testing of restoration interventions and implementation of ecological restoration over larger areas.

Acknowledgements

We are grateful to Table Mountain Fund (1694) and Council for Scientific and Industrial Research for project funding; National Research Foundation/South African Environmental Observation Network, Fynbos Forum/Table Mountain Fund, University of Cape Town, Harry Crossley Foundation and Wilderness Wildlife Safaris Trust for financial support for P. Waller; South African National Parks for permitting; seed collection volunteers; SANBI and Kirstenbosch National Botanical Gardens; Working on Fire Newlands team and Penny Glanville for data from Tygerberg Nature Reserve. The University of Cape Town Statistical Support Team provided considerable guidance and input in analysing the results. We are grateful for the comments of two reviewers who served to improve the final product.

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